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Phylogeography of Bornean land snails suggests long-distance dispersal as a cause of endemism

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Abstract

Aim: Islands are often hotspots of endemism due to their isolation, making colonization a rare event and hence facilitating allopatric speciation. Dispersal usually occurs between nearby locations according to a stepping-stone model. We aimed to reconstruct colonization and speciation processes in an endemic-rich system of land-based islands that does not seem to follow the obvious stepping-stone model of dispersal.

Location: Five land-based habitat archipelagos of limestone outcrops in the floodplain of the Kinabatangan River in Sabah, Malaysian Borneo.

Methods: We studied the phylogeography of three species complexes of endemic land snails, using multiple genetic markers. We calculated genetic distances between populations, applied BEAST2 to reconstruct phylogenies for each taxon and subsequently reconstructed ancestral ranges using 'BioGeoBEARS'.

Results: We found spatial-genetic structure among nearby locations to be highly pronounced for each taxon. Genetic correlation was present at small spatial scales only and disappeared at distances of 5 km and above. Most archipelagos have been colonized from within the region multiple times over the past three million years, in 78% of the cases as a result of long-distance dispersal (LDD) or dispersal from non-adjacent limestone outcrops. The flow of the main geographical feature within the region, the Kinabatangan River, did not play a role.

Main conclusions: Phylogeographic structure in these Bornean land snails has only partly been determined by small-scale dispersal, where it leads to isolation-by-distance, but mostly by LDD. Our results demonstrate that island endemic taxa only very locally follow a simple stepping-stone model, whilst dispersal to non-adjacent islands and especially LDD, is most important. This leads to the formation of highly localized, isolated "endemic populations" forming the onset of a complex radiation of endemic species.

KEYWORDS

Borneo, endemism, Gastropoda, island biogeography, long-distance dispersal, phylogenetics, tropical ecology, tropical land snails



1 | INTRODUCTION

Endemism is often associated with islands (Kier et al., 2009; Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000), where levels can reach impressive values, such as 89.9% in higher plants and 99.9% in land snails in Hawaii (Whittaker & Fernández-Palacios, 2007). On oceanic islands, there is a clear boundary that restricts dispersal. But deserts, mountain tops, lakes and valleys can form habitat islands with many endemics, too (Kruckeberg & Rabinowitz, 1985; Whittaker & Fernández-Palacios, 2007).

The unique research opportunities offered by endemics on islands were already noted by some of the first students of biogeography (Darwin, 1859; Wallace, 1859) and have been exploited ever since (MacArthur & Wilson, 1963; Warren et al., 2015). The probability of a migrant reaching an island from another location generally declines with distance (MacArthur & Wilson, 1963). MacArthur and Wilson's (1967) stepping-stone model detailed possible migration pathways along the chains of islands. Empirical evidence supports the validity of the stepping-stone model in nature as a means of dispersal, such as in marine snails (Crandall, Treml, & Barber, 2012), coastal fish (Gold, Burridge, & Turner, 2001; Maltagliati, 1998) and plants (Harbaugh, Wagner, Allan, & Zimmer, 2009).

Based on the stepping-stone hypothesis, we expect the order and direction of colonization of islands to be of importance in the evolution of island endemics. However, migration resulting from long-distance dispersal (LDD) could result in genetically distant populations becoming neighbours, directly facilitating local endemism. A terrestrial island system in which this idea can be tested is the system of limestone outcrops in the tropical lowlands of Southeast Asia, where acidic soils between outcrops form impassable habitat for species dependent on calcium carbonate (Crowther, 1982; Lim & Kiew, 1997). These species indeed show high levels of local endemism here (Clements, Sodhi, Schilthuizen, & Ng, 2008) and migration of sedentary species between limestone outcrops is considered to be rare (Sodhi, Koh, Brook, & Ng, 2004; Vermeulen & Whitten,

1999). Many are very localized and show a differentiated population structure (Latinne, Waengsothorn, Herbreteau, & Michaux, 2011; Schilthuizen et al., 2006; Sedlock, Jose, Vogt, Paguntalan, & Cariño, 2014). Several studies have shown regional genetic diversity between locations just tens of kilometres apart to be very high (Latinne et al., 2011; Schilthuizen, Vermeulen, Davison, & Gittenberger, 1999). More precise patterns, such as the way in which populations are connected, or the influence of archipelago layout and geology on population structure, remain unstudied.

An abundant and diverse group on these limestone outcrops are land snails (Gastropoda) (Purchon & Solari, 1968; Schilthuizen, 2011; Tweedie, 1961). Local endemism reaches 60% in some sites (Vermeulen & Whitten, 1999). A short generation time (~1 year) and high productivity are possible sources of high levels of genetic variation. The snails' restricted dispersal, combined with bottlenecks and founder effects (Whittaker & Fernández-Palacios, 2007), could form a barrier to the spread of (genetic) variation.

We hypothesized that colonization of limestone outcrops by land snails took place along shortest geographic distances, i.e. following a stepping-stone model. We aimed to reconstruct how endemism emerges from population isolation. We studied spatial and evolutionary genetics of three taxa of regionally common land snail. We collected specimens from 17 different, isolated, limestone outcrops in the Kinabatangan River floodplain in Sabah, Malaysian Borneo (Schilthuizen, Chai, Kimsin, & Vermeulen, 2003). This system offers an opportunity to study both the influence of the grouping of islands and a possible corridor of or barrier to dispersal, the Kinabatangan River.

2 | MATERIALS AND METHODS

2.1 | Study system

We studied three taxa of small land snail (Gastropoda; Figure 1): *Plectostoma concinnum* (Fulton, 1901) s.l., *Georissa similis* E. A. Smith, 1893 s.l. and *Alycaeus jagori* Von Martens, 1859, inhabiting limestone

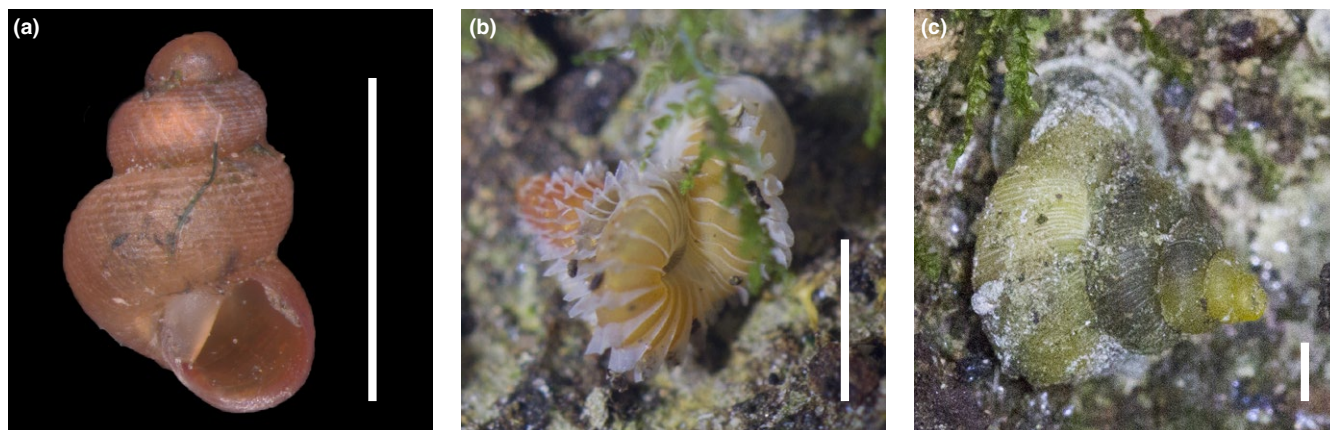


FIGURE 1 Photographs of the target taxa of land snail (Gastropoda) studied. Each taxon is a common inhabitant of the limestone outcrops of the Kinabatangan River floodplain, Sabah, Malaysian Borneo. (a) *Georissa similis* E. A. Smith, 1894, (b) *Plectostoma concinnum* (Fulton, 1901) and (c) *Alycaeus jagori* Von Martens, 1859. Photos: Kasper P. Hendriks. Scale bars equal 1 mm [Colour figure can be viewed at wileyonlinelibrary.com]

outcrops in tropical lowland forest. Ongoing taxonomic studies suggest that the former two taxa are in fact the best considered species complexes (Appendix S1 in Supporting Information). Both are small, with shell heights of 2 and 1 mm respectively (Thompson & Dance, 1983; Vermeulen, 1994), while the latter reaches 10 mm (Kobelt, 1902). Each taxon is locally common (tens to hundreds per square metre) in suitable habitat (Liew, Clements, & Schilthuizen, 2008; Schilthuizen, Rosli, et al., 2003). *Georissa similis* s.l. and *P. concinnum* s.l. are restricted in our study region range (Vermeulen, 1991), while *A. jagori* is distributed all over Sundaland and Sulawesi (van Benthem Jutting, 1948). *Plectostoma concinnum* s.l. is strictly related to calcareous substrate (Schilthuizen et al., 2002), whereas the other two taxa also occasionally occur on trees and shrubs near limestone (personal observations). Studies using standardized plots along a transect that spans both limestone and non-limestone substrate confirm that the “prosobranch” microsnail genera *Plectostoma* and *Georissa* tend to occur nearly strictly on limestone (Schilthuizen, Chai, et al., 2003).

2.2 | Field procedures and sampling

Sampling took place during visits in March 2015 and April 2016. We included additional samples collected with a different purpose during

visits in 2004 and 2017 (Appendix S2). We followed a hierarchical spatial structuring of the region: region>archipelago>outcrop>plot (Figure 2). Five archipelagos (A to E) of limestone outcrops were defined based on a between-outcrop distance of <5 km, with archipelagos of two to seven outcrops. Based on previous studies, we considered dispersal between outcrops to be a rare event (Baur & Baur, 1990, 1995; Cowie, 1984; Schilthuizen et al., 2002). We defined the “population” as the group of individuals from a taxon on one outcrop. We sampled 17 outcrops from at least two plots, with plots on opposite ends of the outcrop. Each plot was 10 m wide (along the periphery of the base of the outcrop) by two metres high. From each plot we aimed to collect 20 individuals of each target taxon at random. Samples were conserved in 98% ethanol.

2.3 | Laboratory procedures

We double-checked identifications of all samples and registered all samples in the molluscan collection of the Naturalis Biodiversity Center, Leiden, the Netherlands (RMNH, samples from 2015) or the BORNEENSIS collection of the Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia (BORN, samples from 2016). We performed whole-DNA extractions on the whole snail (*P. concinnum* s.l. and *G. similis* s.l.) or

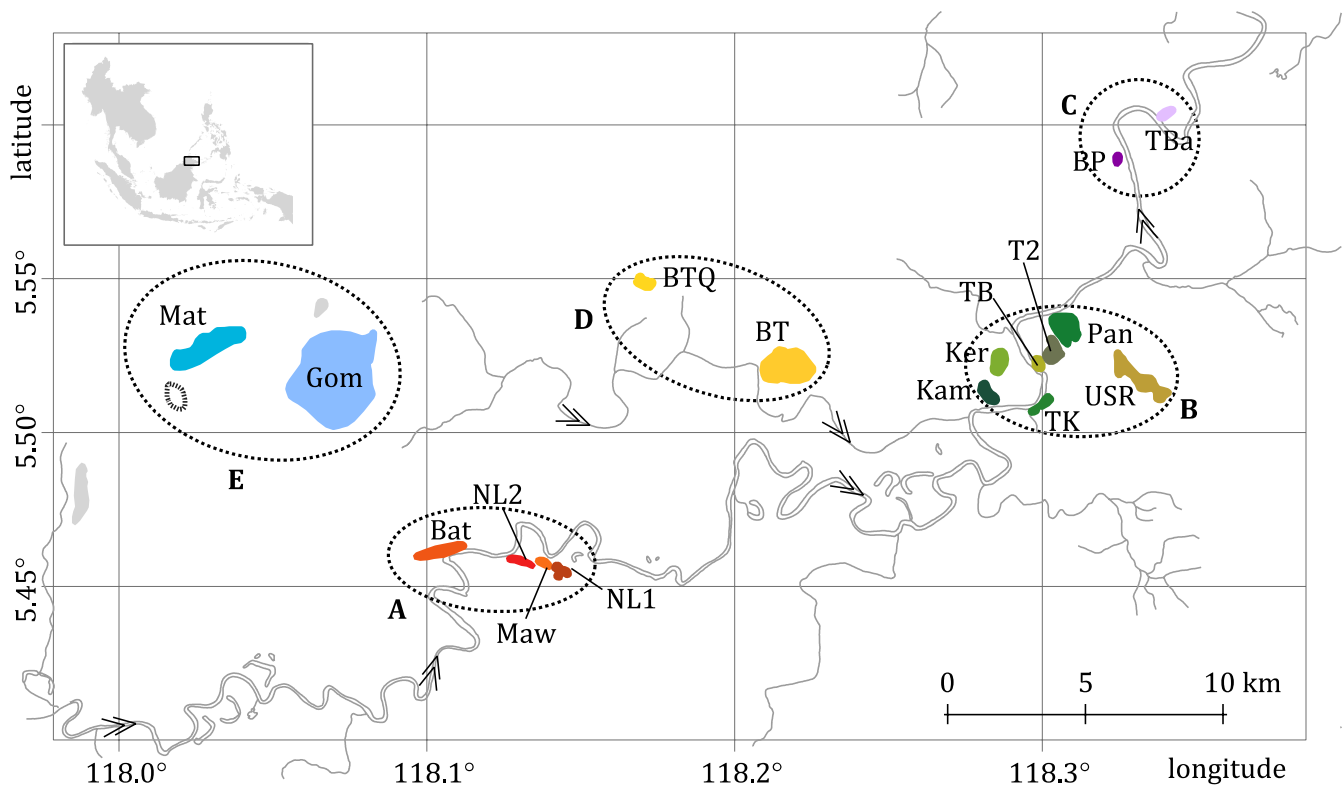


FIGURE 2 Map of the Kinabatangan River floodplain, Sabah, Malaysian Borneo. Habitat islands of limestone outcrops are indicated with different colours and named as follows: Bat (Batangan), Maw (Mawas), NL1 (New Location 1), NL2 (New Location 2), Kam (Kampung), Ker (Keruak), Pan (Pangi), TB (Tomanggong Besar), T2 (Tomanggong 2), TK (Tomanggong Kecil), USR (Ulu Sungai Resang), BP (Batu Payung), TBa (Tandu Batu), BT (Batu Tai), BTQ (Batu Tai Quarry), Gom (Gomantong) and Mat (Materis). Outcrops are grouped by geographical proximity (inter-island distance <5 km) as indicated by dotted ellipses, resulting in archipelagos A to E (shown in bold). The main geographical feature of the region, the Kinabatangan River, is shown in grey, with direction of flow indicated by double arrows. Inset map © Free Vector Maps.com



0.25 g of tissue (*A. jagori*). For extractions of *G. similis* s.l. we used the Macherey-Nagel NucleoMag® Tissue kit on a ThermoFisher KingFisher™ Flex Purification System. For *P. concinnum* s.l. and *A. jagori* extractions were performed using Omega's E.Z.N.A.® Mollusc DNA Kit. We stored all DNA extraction templates at -80°C at the Naturalis Biodiversity Center, Leiden, the Netherlands (Appendix S3).

We used Sanger sequencing to study both mitochondrial and nuclear markers selected from the literature and refer to these publications for details of laboratory procedures. We amplified the mitochondrial cytochrome oxidase I gene (COI) for all taxa and the nuclear Histone 3 gene (H3) for *G. similis* s.l. and *A. jagori*, following Webster, van Dooren, and Schilthuizen (2012). The nuclear internal transcribed spacer 1 region (ITS1) was amplified for *P. concinnum* s.l. and *A. jagori*, following Schilthuizen et al. (2006). We sent amplification products to BaseClear, Leiden, the Netherlands, for sequencing in two directions. We checked sequence reads for errors and deposited all data in the online Barcode of Life Database (BOLD, www.boldsystems.org) as dataset "DS-2018POP" and GenBank (accession numbers in Appendix S3). Due to inconsistent results in forward and reverse sequencing reads in ITS1, which are likely due to within-individual polymorphisms (Vierna, Martínez-Lage, & Gonzalez-Tizon, 2009), we based our analyses of ITS1 on reverse reads only.

2.4 | Population genetic analysis

We studied 929 individual snails (362 *P. concinnum* s.l., 366 *G. similis* s.l. and 201 *A. jagori*). We calculated, by both locus and taxon, nucleotide diversity π (Nei & Li, 1979) and haplotype diversity H_d , at the spatial scale of the outcrop (i.e. the population) and the archipelago. We listed the encountered and normalized (H_{rar}) number of haplotypes. We checked for possible correlations between genetic diversity (π , H_d and H_{rar}) and outcrop "island" area and archipelago size (in terms of sum of outcrop areas and archipelago outcrop number) by applying linear models. Finally, we listed the fraction of private haplotypes, $H_{private}$ (cf. Slatkin, 1985).

To determine metapopulation structure, we calculated between-population fixation indices (Weir & Cockerham, 1984) as Φ_{ST} , a metric that weighs the number of mutations (Bird, Karl, Smouse, & Toonen, 2011; Excoffier, Smouse, & Quattro, 1992). We used the function "pairwiseTest" from R package 'STRATAG' v2.0.2 (Archer, Adams, & Schneiders, 2017), with 1,000 replicates. We also calculated population differentiation as Jost's D (Jost, 2008), using function "pairwise_D" from the R package 'MMOD' v1.3.3 (Winter, 2012). A value of one indicates no shared alleles between two populations (Bird et al., 2011).

We performed an Analysis of MOlecular VAriance (AMOVA; Excoffier et al., 1992) by locus, using the package ARLEQUIN, version WinArl35 (Excoffier & Lischer, 2010). After finding relatively high genetic diversity among outcrops from archipelago A (see Results), we repeated these analyses excluding data from that archipelago and compared results. AMOVA was not performed for *A. jagori* due to insufficient data.

2.5 | Demographic analysis

We studied the spatial component of snail dispersal by relating Jost's D to the shortest geographic distance using Mantel tests (Mantel, 1967) at increasing spatial classes (i.e. geographical distances). We used the function "mantel.correlog" from the R package 'vegan' v2.5-2 (Oksanen et al., 2017), with 15 distance classes and logged Pearson correlations. We summarized results in "Mantel correlograms" (Borcard & Legendre, 2012; Oden & Sokal, 1986).

2.6 | Phylogenetic and biogeographic analyses

We performed Bayesian phylogenetic analysis for each taxon using BEAST2 (Bouckaert et al., 2014) with trees for each locus ("gene trees") linked to conform to the taxon tree ("species tree") and clock and site models unlinked. The site model for each locus followed output from JMODELTEST2 (Darriba, Taboada, Doallo, & Posada, 2012) and analyses were repeated with a general GTR site model. We set a strict clock for each locus, which is appropriate in the study of closely related taxa (Brown & Yang, 2011), with a clock rate of 2% per million years for COI (Nekola, Coles, & Bergthorsson, 2009; Wares & Cunningham, 2001). With no clock rate estimates available for the other loci, the software estimated rates for these relative to that for COI. We set a Yule tree prior. We ran analyses for 100 million generations, sampling posterior parameter values and trees every 10,000th generation, after which we discarded a 10% burn-in. We checked convergence for each run based on ESS values >200 and proper mixing of parameters over time. We summarized trees with a posterior probability limit of 50%. We compared model results by Bayes Factor (BF; based on the harmonic mean of the log-likelihood of the posterior), and chose the model with the highest BF (Suchard, Weiss, & Sinsheimer, 2001) or, when the BF was zero, the model with the highest posterior probabilities of tree clades. (A better, more intensive model selection method, using nested sampling, was published during time of writing [Maturana, Brewer, Klaere, & Bouckaert, 2017]. We expect model selection not to be different when large absolute BFs are found.) All BEAST2 runs were performed on the CIPRES computing cluster (Miller, Pfeiffer, & Schwartz, 2010).

We calculated probabilities of possible ancestral ranges for each taxon using the R package 'BioGeoBEARS' v0.2.1 (Matzke, 2013) with a maximum likelihood approach. We pruned the phylogeny to "species" level for each taxon by randomly selecting a single sample from each phylogenetic clade for each outcrop to represent the "species". Possible ancestral range size was set to "current range size plus one" to allow for larger historical ranges. One exception was a large clade in *A. jagori*, which consisted of samples from four different outcrops. We accounted for this by setting the current range for this "species" to "four" instead of "one". To allow for "founder-event speciation" and based on our understanding of a jumping mode of "speciation" in these island endemic snails (i.e. by colonization of new outcrops), we selected the DEC+J model in our analyses (Matzke, 2014). Concerns raised by Ree and Sanmartin (2018) on the DEC+J model are unlikely to have any significant effect on our

results due to the strong spatial structure in our system. We scored dispersal and colonization events as follows: LDD (with separation between downriver and upriver), within-archipelago (but not to adjacent outcrop or crossing the river) and stepping-stone (to adjacent outcrop). Based on the high genetic affinities found within the outcrop in each species complex, we did not include the possibility of ancestral ranges being smaller than the outcrop.

Finally, we repeated the demographic test of the Mantel correlogram, now using a mean pairwise phylogenetic distance between samples per population (c.f. Cadotte & Davies, 2016, p. 48) as measure of genetic differentiation.

3 | RESULTS

We sampled the target land snails, *P. concinnum* s.l., *G. similis* s.l. and *A. jagori*, from the following 17 limestone outcrops (with numbers for each in brackets respectively): Batangan (21, 3, 0), Mawas (29, 20, 0), New Location 1 (30, 9, 0), New Location 2 (43, 0, 0), Kampung (25, 28, 0), Keruak (27, 28, 0), Pangi (30, 43, 45), Tomanggong Besar (30, 28, 27), Tomanggong 2 (5, 40, 28), Tomanggong Kecil (29, 46, 23), Ulu Sungai Resang (0, 28, 0), Batu Payung (28, 15, 17), Tandu Batu (39,

28, 30), Batu Tai (0, 29, 0), Batu Tai Quarry (9, 1, 16), Gomantong (16, 7, 0) and Materis (0, 13, 15). *A. jagori* was not found from outcrops in archipelago A and is likely to be absent from these hills. Voucher and museum identification numbers are listed in Appendix S3.

3.1 | Population genetic analysis

Nei's π was highest in *G. similis* s.l. and lowest in *A. jagori* (Figure 3a; Appendix S4). In *G. similis* s.l., data from both markers showed a relatively high π for populations from archipelago E, while the other two taxa showed low values for this archipelago. COI data in *P. concinnum* s.l. showed high values of π for archipelago C (cf. Schilthuizen et al., 2006).

H_{rar} was highest for archipelago B (Figure 3b; Appendix S4). Haplotype diversity was very similar for each taxon, with the highest values for archipelago B (Appendix S4). We found little correlation between genetic diversity and outcrop or archipelago area or archipelago outcrop number (Appendix S5). There were positive trends between archipelago outcrop number and H_{d} , but correlations were non-significant (possibly due to a small number of data points). We found H_{private} to be very high for all three taxa, all populations/archipelagos and all loci (Appendix S4), indicating haplotypes rarely occurred in more than one archipelago.

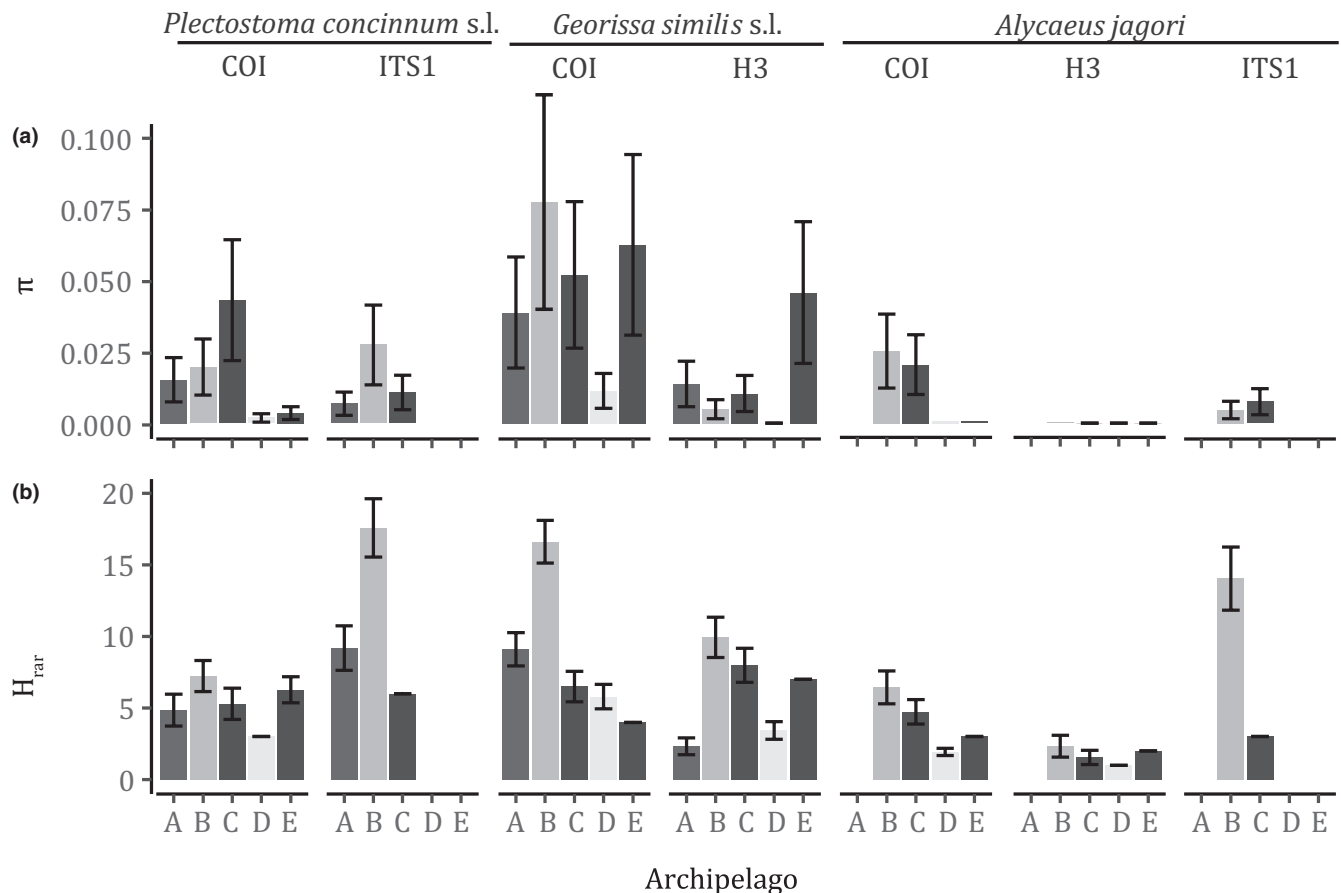


FIGURE 3 (a) Nucleotide diversity π (Nei & Li, 1979) and (b) number of haplotypes based on rarefaction, H_{rar} , for *Plectostoma concinnum* s.l., *Georissa similis* s.l. and *Alycaeus jagori*, grouped by genetic marker and by archipelago (A to E) in the Kinabatangan River floodplain. Error bars represent standard deviations

TABLE 1 Results of Analyses of MOlecular VAriance (AMOVA; Excoffier et al., 1992), by genetic marker, for *Plectostoma concinnum* s.l. and *Georissa similis* s.l. Sample grouping followed the hierarchical structuring of the region (region>archipelago>outcrop [~population]). Values in parentheses are for the alternative case in which data from archipelago A were excluded. Abbreviations: *df* (degrees of freedom), *SS* (sum of squares), *PV* (percentage of variation). Significance tests: **p* < 0.05, ***p* < 0.005

	COI			ITS1			H3		
	<i>df</i>	<i>SS</i>	<i>PV</i>	Fixation index	<i>df</i>	<i>SS</i>	<i>PV</i>	Fixation index	Fixation Index
<i>Plectostoma concinnum</i> s.l.									
Among archipelagos	4 (3)	3281 (1524)	38.7 (20.5)	0.884** (0.875)**	2 (1)	1285 (850)	38.4 (37.5)	0.820** (0.919)**	
Populations within archipelagos	9 (6)	2970 (2390)	54.2 (69.6)	0.381** (0.205)**	9 (6)	1173 (1007)	50.5 (51.1)	0.384** (0.375)**	
Within populations	329 (216)	559 (506)	7.1 (9.9)		198 (122)	368 (339)	11.1 (11.4)		
Total				0.929** (0.901)**				0.889** (0.887)**	
<i>Georissa similis</i> s.l.									
Among archipelagos	4 (3)	3249 (2301)	18.5 (17.3)	0.806* (0.788**)					4 (3) 191 (170) 36.4 (44.7) 0.792** (0.777**)
Populations within archipelagos	11 (9)	5854 (5029)	65.7 (65.2)	0.185** (0.173*)					11 (9) 243 (214) 50.4 (42.9) 0.363** (0.447*)
Within populations	344 (315)	1946 (1835)	15.8 (17.6)						264 (239) 83 (79) 13.2 (12.4)
Total				0.842** (0.825**)					0.868* (0.876**)

Fixation indices Φ_{ST} (based on a combination of all loci studied) were generally moderate between populations within archipelagos and high between populations from different archipelagos (Appendix S6). Mean within-archipelago values (excluding non-significant values) for *P. concinnum* s.l., *G. similis* s.l. and *A. jagori* were 0.046, 0.024 and 0.045 respectively; between-archipelago means were 0.113, 0.034 and 0.079. Thus, populations are, at least on average, more closely related at the spatial scale of the archipelago and less so at a larger scale. Fixation indices between populations from archipelago A and other archipelagos were among the highest values found overall.

Mean within-archipelago values of Jost's *D* were 0.588, 0.673 and 0.327 for *P. concinnum* s.l., *G. similis* s.l. and *A. jagori* respectively; between-archipelago means were 0.592, 0.764 and 0.743 (Appendix S6). This means that genetic differentiation was only slightly higher between than within archipelagos for the first two taxa; for *A. jagori* differentiation is much stronger between archipelagos, indicating closer relationships between populations within archipelagos. Values between archipelago A and all other archipelagos are higher than the averages reported above: 0.649 for *P. concinnum* s.l. and 0.942 for *G. similis* s.l., indicating that on average archipelago A was genetically most distinct.

The AMOVA analyses revealed that most of the genetic variation present (PV) was at the level of "populations within an archipelago" (50.4%–65.7%; Table 1). Remaining genetic variation was explained mostly by "among-archipelago" differences (18.5%–38.7%). The last portion of variation was ascribed to genetic

differences "within populations" (7.1%–15.8%). These results show that there were large genetic differences between populations within each archipelago. When repeating the AMOVA analyses while excluding data from archipelago A (results within parentheses in Table 1), "populations within an archipelago" now explained 69.6% for *P. concinnum* s.l. COI marker (vs. 54.2% for the full dataset); we found no difference for the ITS1 marker. For *G. similis* s.l., results for the COI marker were virtually identical (65.7% for full dataset, versus 65.2% when excluding archipelago A), but for H3 values instead dropped (50.4% for the full dataset, vs. 42.9% excluding archipelago A). Overall, the pattern found from the alternative dataset was similar, with most variation explained by the level of "populations within an archipelago".

3.2 | Demographic analysis

We found a significantly positive correlation between genetic fixation and geographic distance for *A. jagori*, but only up to 5 km geographic distance (i.e. within archipelagos); correlations for *P. concinnum* s.l. and *G. similis* s.l. were close to zero (Figure 4a; Digital Supporting Information 1).

3.3 | Phylogenetic and biogeographic analyses

We chose phylogenetic results from BEAST2 for each species complex based on models with maximum BF (Appendix S7). Our phylogenetic studies showed that individual snails from the same outcrop

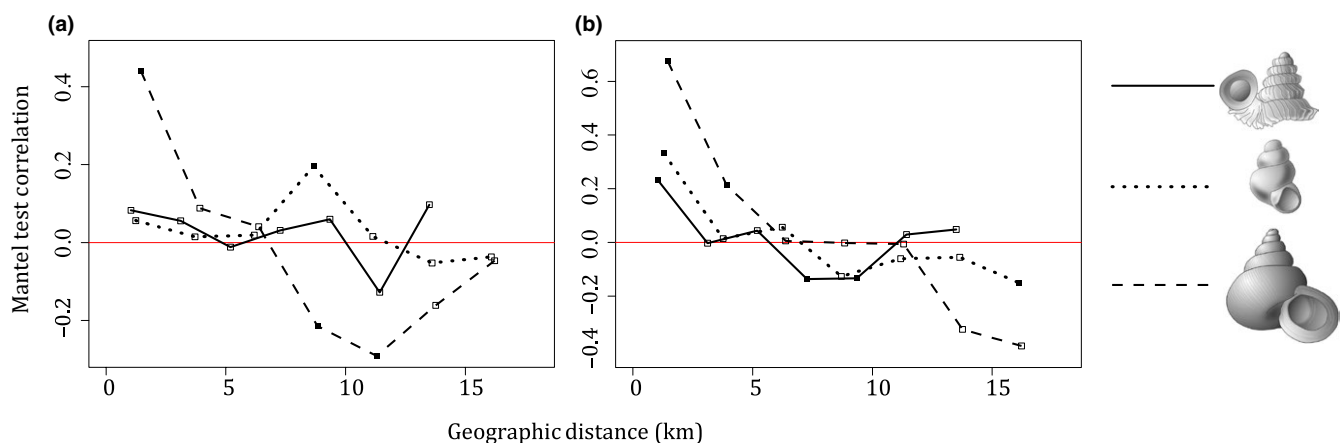
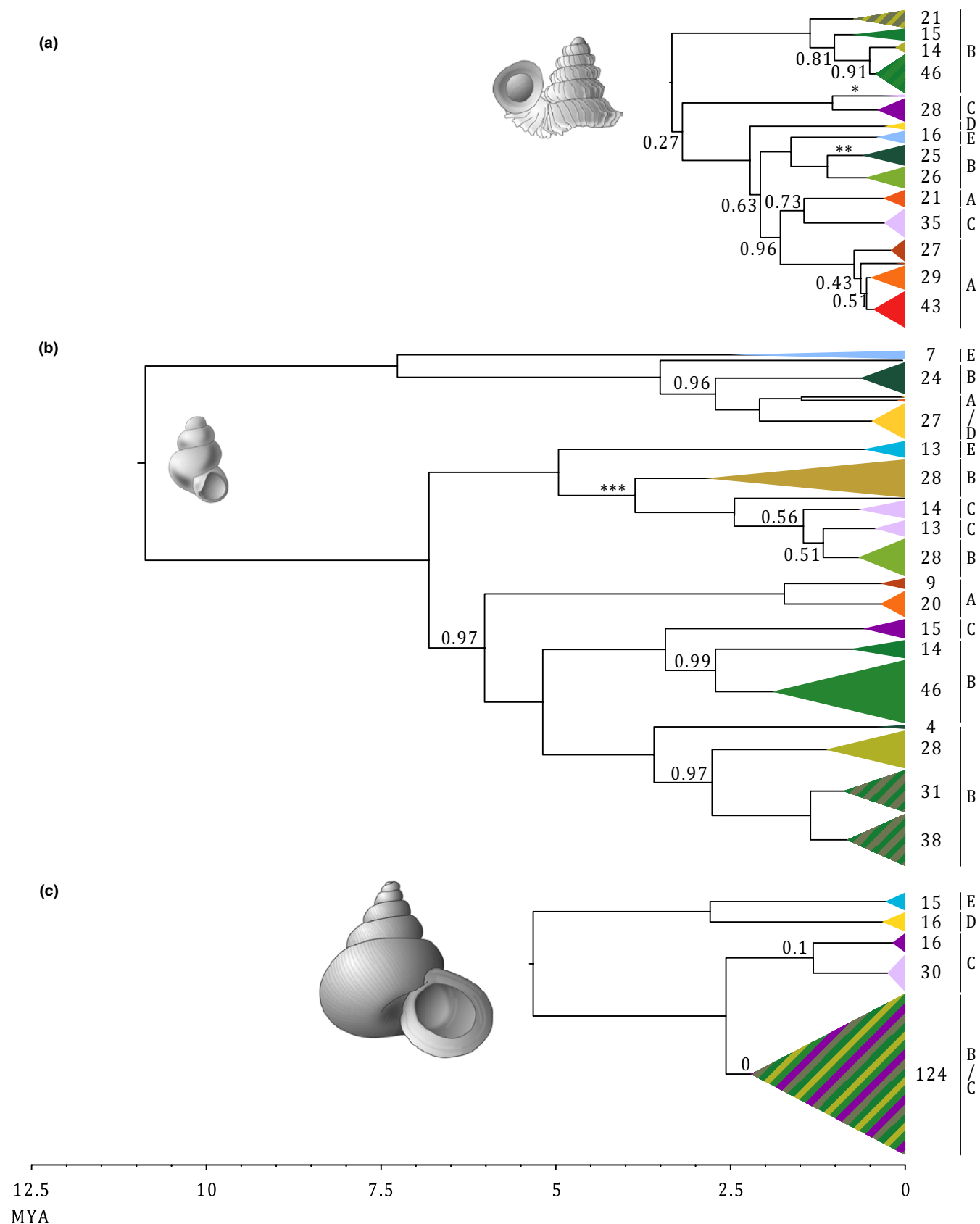


FIGURE 4 Mantel correlograms for the three taxa studied, *Plectostoma concinnum* s.l., *Georissa similis* s.l. and *Alycaeus jagori*. Mantel test correlations (Pearson method) are plotted versus geographic distance. Positive values indicate positive correlations between genetic and geographic distances; black squares indicate significant values. (a) Correlations tested on genetic differentiation, using Jost's *D* (Jost, 2008); (b) Correlations tested on a mean pairwise phylogenetic distance between samples per population. Inset artwork: Bas Blankevoort, Naturalis Biodiversity Center [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 Results of phylogenetic analyses using BEAST2 for (a) *Plectostoma concinnum* s.l., based on COI and ITS1 markers; (b) *Georissa similis* s.l., based on COI and H3 markers; and (c) *Alycaeus jagori*, based on COI, ITS1 and H3 markers. Colours of tip nodes correspond to the different outcrops (for which see Figure 2). Width of tip nodes is scaled to genetic diversity within the respective clade. Height and numbers at the tips represent sample size, letters indicate archipelagos. Posterior probability values of the clades are 1, unless indicated at the node. Previously published morpho-species are indicated as follows: **P. simplex* (Fulton, 1901), ***P. mirabile* (Smith, 1893) and ****G. nephrostoma* Vermeulen, Liew & Schilthuis (2015) (see Appendix S1 for details). Full phylogenetic trees can be found in Appendix S8. Inset artwork: Bas Blankevoort, Naturalis Biodiversity Center



are genetically closely related, with a few exceptions (Appendix S8). At the scale of the archipelago, we often found more than one genetic clade (three times in *P. concinnum* s.l., five times in *G.*

similis s.l. and once in *A. jagori*; Figure 5). As a result, populations on neighbouring outcrops, just several hundred metres apart, are often not each other's closest relatives.

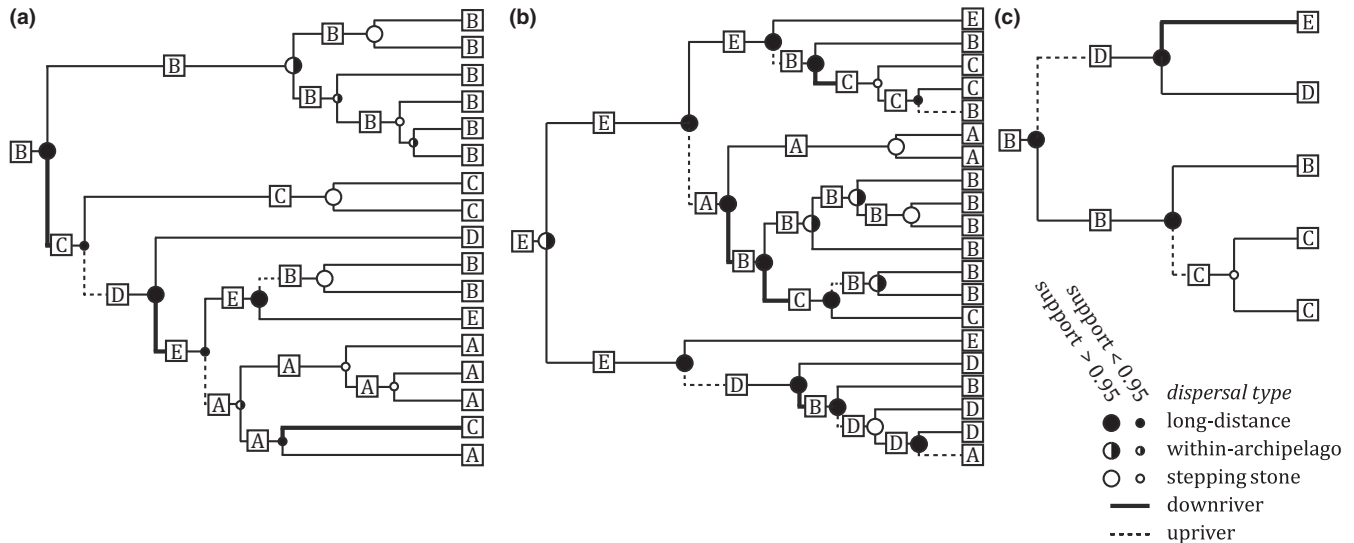


FIGURE 6 Results of ancestral range reconstructions using the R package 'BioGeoBEARS' for (a) *Plectostoma concinnum* s.l., (b) *Georissa similis* s.l. and (c) *Alycaeus jagori*. Letters with each (ancestral) lineage refer to the archipelago found as most likely range. Dispersal type with each dispersal and colonization event is indicated by a filled (long-distance), half filled (crossing the river or to a non-adjacent outcrop) or open (stepping-stone, i.e. to adjacent outcrop only) circle. Large circles represent "speciation events" with a posterior support of $\geq 95\%$; small circles have a support of $< 95\%$. With each long-distance dispersal event, line type indicates a downriver (bold line) or upriver (dashed line) dispersal event. Reconstructions follow the phylogenies from Figure 5 pruned to "species" level for each species complex. For full BioGeoBEARS output, see Appendix S9

TABLE 2 Counts of dispersal and colonization events for each of the three species complexes studied, *Plectostoma concinnum* s.l., *Georissa similis* s.l. and *Alycaeus jagori*. We distinguished long-distance dispersal, within-archipelago dispersal (crossing the river or to a non-adjacent outcrop) and stepping-stone dispersal (to adjacent outcrop only). Counts of downriver and upriver dispersal and colonization events are given. Only "speciation events" with a posterior support of $\geq 95\%$ included; numbers within brackets include all "speciation events"

Dispersal type/taxon	<i>Plectostoma concinnum</i> s.l.	<i>Georissa similis</i> s.l.	<i>Alycaeus jagori</i>
Long-distance	3 (6)	10 (11)	3 (3)
Within-archipelago	1 (4)	4 (4)	0 (0)
Stepping stone	3 (6)	3 (4)	0 (1)
Downriver	2 (3)	4 (4)	1 (1)
Upriver	1 (3)	6 (7)	2 (2)
Total speciation events	7 (16)	17 (19)	3 (4)

We estimated most genetic clades in *P. concinnum* s.l. to have originated around 1 Ma (mean clade age 1.15 ± 0.53 Ma). In *G. similis* s.l. (2.67 ± 1.06 Ma) and *A. jagori* (2.14 ± 0.67) populations were older. It should be noted that mutation rates can actually differ substantially between these three distantly related taxa, which would alter (relative) clade ages.

Calculations of most probable ancestral ranges showed different patterns for the different species complexes. (Figure 6; for full output see Appendix S9). Colonization and the origin of new genetic lineages were commonly associated with dispersal to non-adjacent outcrops (LDD and within-archipelago dispersal), making up 4 out of 7, 14 out of 17 and 3 out of 3 "speciation events" in *P. concinnum* s.l., *G. similis* s.l. and *A. jagori* respectively (Figure 6; Table 2; based on significantly supported clades only). Stepping-stone dispersal was found to be

uncommon in each of the three species complexes studied (rest of the "speciation events"). Long-distance dispersal was slightly more common in an upriver than downriver direction (9 vs. 7 cases respectively).

The repeated demographic Mantel test, using mean pairwise phylogenetic distances between samples per population, pointed at spatial-genetic relationships being positive up to 3–5 km distance between populations, with the most pronounced result for *A. jagori* (Figure 4b).

4 | DISCUSSION

Our results show that spatial-genetic structure of land snails in the Kinabatangan River floodplain is composed of two forms: local structure, as isolation-by-distance, suggesting a stepping-stone model



between nearby habitat islands and regional structure, with random connections between more distant populations. This is true for all three species complexes studied, with haplotype diversity and haplotype numbers being highest within archipelago B, which has the highest number of outcrops. The patterns found are the strongest for *P. concinnum* s.l. and *G. similis* s.l., while *A. jagori* shows relatively higher local dispersal, which is in agreement with its more generalist character, being found more often away from limestone. We found positive, non-significant correlations between haplotype diversity and archipelago island number. Most of the genetic diversity can be explained by the spatial scale of "populations within an archipelago", as supported by both AMOVA and Φ_{ST} -values. Archipelago A is genetically most isolated. Most archipelagos have been colonized multiple times from within the region. Colonization through LDD and within-archipelago dispersal (i.e. non-stepping-stone dispersal) is associated with 78% of the "speciation events", highlighting the importance of dispersal over long distances in the origin of endemism in our system.

We find genetic diversity to vary with both taxon and archipelago (Figure 3; Appendix S4). Patterns in H_{rar} values are broadly consistent between all three taxa and markers, with the highest values for archipelago B. An explanation may be the larger island number and island size in archipelago B (Appendix S5). Within each outcrop, snails will encounter a matrix of suitable and unsuitable microhabitats. Larger outcrops will have a higher number of such suitable microhabitats, which likely results in more genetic diversity within the outcrop ("islands within islands", cf. Holland & Hadfield, 2002).

An explanation for the difference in haplotype diversity between taxa and outcrops may be the difference in age of the various populations. Bottlenecks (due to a small number of colonizing individuals) and subsequent founder effects are considered important consequences of island colonization events (Whittaker & Fernández-Palacios, 2007, p. 168) and results include low genetic diversity and chance effects in the sorting of alleles. Therefore, low haplotype diversity may simply indicate a relatively young local population.

A combined effect of local dispersal and LDD, as we found in our system, was also described by Crandall et al. (2012) for marine snails. In studies on the limestone-dwelling snail *Gylotrichela hungerfordiana* (von Moellendorff, 1891) of Peninsular Malaysia, a similar pattern was found (Hoekstra & Schilthuizen, 2011; Schilthuizen et al., 1999) in which dispersal acts in two different forms: "successive colonization of ever further limestone outcrops" and "additional long-range dispersal", where the latter is infrequent. While for *G. hungerfordiana* this pattern was shown at the spatial scale of 100s of km, here we find it at a scale of just 30 km. This difference may be explained by the nature of the habitat (smaller outcrops in our study) and the difference in size of the animals themselves (*G. similis* s.l. and *P. concinnum* s.l. being considerably smaller than *G. hungerfordiana*).

Long-distance dispersal is usually considered rare and difficult to describe scientifically (but see e.g. Nathan, 2006). Nonetheless, snails are, perhaps paradoxically, among the most successful colonizers of islands, including oceanic islands far offshore, such as the Galápagos (Parent & Crespi, 2006), Hawaii (Rundell, Holland, & Cowie, 2004), Norfolk Island (Donald, Winter, Ashcroft, & Spencer,

2015) and Madeira (Waldén, 1983). Interesting overviews of possible LDD vectors in land snails are given by Purchon (1977, p. 335) and Dörge, Walther, Beinlich, and Plachter (1999). Two natural passive dispersal possibilities discussed by Dörge et al. (1999) may shed some light on our system. The first is running water, the combination of heavy tropical showers and the proximity of the regularly flooding Kinabatangan River (Estes et al., 2012) our system amply offers. Dörge et al. (1999) make special mention of the observations made by Boettger (1926) and Czögler and Rotarides (1938) of large numbers of land snails found in driftwood. However, we found that dispersal took place in both downriver and upriver directions. The second possibility, of passive dispersal by other animals, may be more likely. Both observations (Brandes, 1951) and experiments (van Leeuwen & van der Velde, 2012) have shown that snails can attach to bird feathers and survive for some time inside the gut of birds after having been swallowed (N. Matzke, 1962; van Leeuwen, van der Velde, van Groenendael, & Klaassen, 2012; Wada, Kawakami, & Chiba, 2012). We expect other animals, such as wild boar and primates, to be other likely dispersal vectors.

In this study, we have shown that populations of locally common taxa, by means of LDD, can reach distant islands. When reaching such new territory, these populations are likely to be genetically distinct from their neighbouring conspecifics, which can result in local endemic species. When this happens multiple times (but not too often) in a small region, such as the Kinabatangan Floodplain, the result is a radiation of highly localized endemics. Set in a geographically complex habitat island system, we see here the ongoing evolution of several species complexes of endemic land snails.

Karst habitats in Southeast Asia have been dubbed "biodiversity hotspots" (Hughes, 2017). Due to anthropogenic activities, such as quarrying, mining, deforestation and tourist industry, limestone outcrops in Southeast Asia are rapidly disappearing (Hughes, 2017; Sodhi et al., 2010). With many inhabiting species being endemic, the disappearance of each limestone outcrop results in the extinction of species, possibly including ones that have not yet been scientifically described. This is true for our study area and our study system of small land snails (Clements et al., 2008). The result is genetic depletion (Harrison & Hastings, 1996), possibly reducing species survival chances (Simberloff, 1988). It is important to understand and conserve the genetic complexities of the uniquely high levels of endemism we find in these island systems.

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DATA ACCESSIBILITY

All sample DNA sequence and metadata are publicly available online as a single dataset ("DS-2018POP") through the Barcode of Life Database (BOLD), www.boldsystems.org, or <http://dx.doi.org/10.5883/DS-2018POP>. Sequence data are also available from GenBank; see Appendix S3 for accession numbers. All DNA extractions (templates) are stored at the DNA barcoding facility of Naturalis Biodiversity Center (NBC), Leiden, the Netherlands, at -80°C , for future reference (see Appendix S3 for details).

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Author contributions: K.P.H. & G.A. collected samples in the field, performed genetic laboratory work and analysed the data; K.P.H. led the writing, with input from all authors; R.S.E. and M.S. conceived original project ideas.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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